Seasonal variations in the basal rate of metabolism of subtropical insectivorous bats (*Nycticeius humeralis* and *Lasiurus seminolus*): a comparison with other mammals

by

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With 3 figures

ABSTRACT

The basal rate of metabolism of the evening bat *(Nycticeius humeralis)* and the seminole bat *(Lasiurus seminolus)* was measured at various times of the year, and its seasonal variation was compared with that of other mammals. The BMR of both species is lower than predicted on the basis of body mass (resp. 52% and 65% of expected). It shows a seasonal variation with a low during the autumn-winter period, when the foraging activity of the bats is limited. Seasonal changes in body mass and/or adiposity are unable to explain this variation. The seasonal variation observed in *Nycticeius* and *Lasiurus* is similar to that exhibited by hibernators as opposed to that shown by several small non-hibernating mammals living in cold habitats and by species inhabiting hot environments. Food accessibility and climate, two factors that are thought to explain much of the interspecific variability in mammalian BMR, also appear to be important factors influencing the pattern of intraspecific seasonal variation.

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INTRODUCTION

The basal rate of metabolism (BMR) of mammals shows great variability, mostly due to variations in body mass (KLEIBER 1961). However, if the influence of mass is eliminated, significant variation remains (MCNAB 1986, ELGAR & HARVEY 1987). Food habits and climate are among the most important factors that have been suggested to explain this residual variation. In general, low food accessibility (MCNAB 1986) and the risk of overheating in a hot environment (MCNAB 1966, 1979a, b, MACMILLEN & LEE 1970) are thought to favour a reduced rate of metabolism, whereas a high reproductive output (MCNAB 1980, HENNEMANN 1983) and the ability to maintain continuous endothermy (MCNAB 1983) may be major advantages derived from a high rate of metabolism.

Climate and food availability vary seasonally in most habitats. Therefore, one may expect selective pressures to vary along the year. To what extent the rate of metabolism can track these seasonal variations certainly depends partly on physiological and biochemical constraints, but at least, the comparative study of seasonal variations in the BMR may shed light on some of the ecological factors that are responsible for the residual variation in mammalian BMR. A seasonal variation in mass-specific BMR has been documented in a number of mammals, including several hibernators (KAYSER 1965, HILDWEIN 1970), small species of cold and seasonal environments (LYNCH 1973, WUNDER et al. 1977, MERRITT 1986), as well as species inhabiting warm habitats (HILDWEIN 1972, HINDS 1973, 1977, ZERVANOS 1975, ROSS 1980, GOLIGHTLY & OHMART 1983). In other mammals, no seasonal variation has been observed (IRVING et al. 1955, GORECKI 1966, 1969, ROSENMANN et al. 1975).

Insectivorous bats from temperate and subtropical regions exhibit a strong seasonality in their life history patterns (see BARBOUR & DAVIS 1969, for American bats). They are actively foraging during most nights in spring and summer, when the energetically most expensive processes associated with reproduction take place. In contrast, during the winter or autumn-winter period, when ambient temperatures are lower and the insect prey are much less abundant, they strongly reduce their activity and undergo extended periods of torpor, unless they migrate to warmer regions. Adaptations limiting the rate of energy use should be of value during this period of low food availability.

The evening bat *(Nycticeius humeralis)* and the seminole bat *(Lasiurus seminolus)* are two Vespertilionidae common in the southeastern United States (BARBOUR & DAVIS 1969). In subtropical regions (northern Florida), the winter climate is rather mild, but between December and March, cold spells lasting several days typically alternate with milder periods. During these cold spells, the evening temperature is often too low to permit efficient foraging. Both species are able to enter torpor. However, the thermal conditions in subtropical regions should lead to relatively high energy expenses during torpor, compared to those of species hibernating in more northern regions. In this paper, the hypothesis that the BMR of evening bats and seminole bats is reduced during the period of limited foraging activity will be tested, and the seasonal variation observed in *N. humeralis* and *L. seminolus* will be compared with that exhibited by other mammals.

MATERIAL AND METHODS

SEASONAL GROUPS

For each species, two seasonal groups were defined (groups 1 and 2), in order to distinguish the period of the year where the bats are actively foraging during most of the nights from the period where they exhibit a strongly reduced flight activity. These groups were established on the basis of data taken from the literature. *N. humeralis* and *L. seminolus* exhibit different overwintering strategies, resulting in different seasonal groups for the two species. The evening bat stores large amounts of fat in August (BAKER *et al.* 1968). It strongly reduces its foraging activity during autumn and winter, as is shown by results of public shots (JENNINGS 1958) and direct observations (BAIN & HUMPHREY 1986). In contrast, *L. seminolus* remains active throughout the winter, but direct observations revealed that seminole bats seldom fly when ambient temperature is below 13° C (CONSTANTINE 1958, JENNINGS 1958). In subtropical Florida, this typically occurs during cold spells. Thus in *N. humeralis,* bats caught between April and August were assigned to group 1 and those caught between September and March to group 2. In *L. seminolus,* individuals netted between April and November were assigned to group 1 and those netted between December and March to group 2.

ANIMALS

Twenty-four *N. humeralis* and 19 *L. seminolus* were used for this study. The evening bats were either netted over creeks and ponds in northern Florida (10 individuals, counties of Alachua, Columbia and Marion), or captured by hand in attics (13 individuals from Citrus County and one from Captiva Island, Lee County). Except the single individual from Captiva Island, which belonged to the subspecies *N. h. subtropicalis,* all evening bats belonged to the subspecies *N. h. humeralis.* Eighteen of these evening bats (group 1) were caught between April and July (1984 and 1985), and the other six (group 2) between September and December 1984. The seminole bats were netted at all seasons between April 1984 and June 1985 over the same places as the evening bats. Nine of them were assigned to group 1 and the 10 others to group 2.

The bats could be maintained in captivity for up to five months, but all measurements were made during the same month as capture. The social organization of each species (BARBOUR & DAVIS 1969) was taken into account to define the captivity conditions: evening bats were maintained in small groups (up to ten individuals) in a cage whereas the seminole bats were kept in large individual cloth bags. All bats were kept under a natural photoperiod regime and at an ambient temperature ranging between 20° C and 24° C. They were hand-fed three times each night with mealworms and a vitamin supplement for insectivores, and were allowed to fly in a room every other evening. Except for pregnant females, the bats remained within a range of 1.5 g around their initial body weight, and most of them were released at the capture site at the end of the experiments.

RESPIROMETRIC MEASUREMENTS

The rate of metabolism was measured in an open air-flow respirometer, under dim light and between 1100 h and 1900 h. Prior to the measurements, the bats were left without food for at least 6 h to be postabsorptive. They were placed in a 1 l metabolic chamber which was submersed in a water bath at a regulated temperature. A vertical screen and small branches at the top of the chamber allowed the bats to roost in their natural posture:

N. humeralis clinged to the screen, and *L. seminolus* remained suspended at the top. Air temperature within the metabolic chamber was measured with a thermocouple connected to a telethermometer (BAT-8, Bailey Instruments, NJ, USA).

Air was provided by a pump at a regulated flow (35-175 ml/min). After the chamber, the air was passed through a CO_2 trap (soda lime), and a water trap (color indicator silica gel). Downstream of these traps, the flow rate was measured with flowmeters (Sho-Rate R-2-15 A, AA and AAA, Brooks, PA, USA), which were calibrated with the same calibrator (Vol-U-Meter gas calibrator, Brooks). The oxygen concentration was measured with an Applied Electrochemistry Oxygen analyzer (Ametek, PA, USA) and was continuously recorded.

Bats were left for an initial period of 2 h to adjust to the chamber. After this period, a measurement was retained only if it corresponded to 30 min of total immobility, a condition that was associated with a constant oxygen concentration after the chamber. Oxygen consumption was calculated according to DEPOCAS & HART (1957; equation 10), the concentration of the inlet air being obtained without the animals, before and after the runs. All values were corrected to STP conditions.

In both evening and seminole bats the thermoneutral zone ranges from about 32° C to about 36° C, as was shown by a thorough study of their rate of metabolism and thermoregulatory abilities at various ambient temperatures (results to be published elsewhere). Therefore, minimal values obtained at an ambient temperature of 35° C ($\pm 0.5°$ C) were taken as estimates of the BMR for both species. Furthermore, females with an advanced pregnancy (pregnancy detectable by palpation and large body weight) were not included in this study.

DATA ANALYSIS

Since a sexual dimorphism in body mass is typical of both species (BARBOUR & DAVIS 1969, WILKINS 1987), a sexual dimorphism in the BMR was *a priori* considered as plausible. Therefore, not only season and body mass, but also sex were considered as possible sources of intraspecific variation in the BMR. For each individual, the BMR was expressed as a mass-specific rate. When several measurements were available for the same individual, an average value was retained. The effect of body mass was then eliminated by expressing the BMR as a percentage of the value expected from different allometric equations (e.g. KLEIBER 1961, HEUSNER 1982). Calculating these percentages from mass-specific or absolute BMR data leads to identical values. Analyses of variance (ANOVA, SOKAL & ROHLF 1981) were performed on these mass-independent BMR estimates, using a two factor unbalanced factorial model controlling for the factors sex and season.

RESULTS

NYCTICEUS HUMERALIS

As expected, the body mass of *N. humeralis* varied according to season ($F = 43.1$, $P < 0.001$) and sex ($F = 34.1$, $P < 0.001$; interaction term sex * season not significant, $F = 0.03$, $P > 0.05$). Bats of group 2 were heavier than those of group 1, due to the large amounts of fat accumulated since the end of the summer, and females tended to be heavier than males (Table 1). The BMR ranged between 0.73 and 1.51 mlO$_2$/gh. It was generally lower in group 2 than in group 1 (Table 1 and Fig. 1), but the effect of body mass has to be taken into account to interpret this seasonal difference.

TABLE 1.

Basal rate of metabolism (BMR) of *Nycticeius humeralis* and *Lasiurus seminolus* in groups 1 and 2. Standard deviations and number of individuals (*n*) are indicated.

		Group 1			Group 2		
		BMR (mlO$_2$/gh)	body mass (g)	*n*	BMR (mlO$_2$/gh)	body mass (g)	*n*
N. humeralis	all	1.19 ± 0.15	9.02 ± 1.10	18	0.82 ± 0.13	11.09 ± 1.04	6
	females	1.13 ± 0.11	9.54 ± 0.60	13	0.84 ± 0.15	11.75 ± 0.29	4
	males	1.33 ± 0.16	7.68 ± 0.97	5	0.78 ± 0.07	9.78 ± 0.11	2
L. seminolus	all	1.38 ± 0.12	9.75 ± 1.32	9	1.15 ± 0.13	9.02 ± 1.00	10
	females	1.26 ± 0.09	11.34 ± 0.45	3	1.07 ± 0.05	9.63 ± 0.09	3
	males	1.44 ± 0.08	8.95 ± 0.66	6	1.18 ± 0.14	8.75 ± 1.11	7

The influence of mass can be eliminated by expressing the measured rates as a percentage of the values expected from the KLEIBER (1961) scaling relationship BMR = 3.42 $m^{-0.25}$ (BMR in mlO$_2$/gh and *m* in g) (Fig. 1). The scaled BMR significantly depends on season ($F = 31.9$, $P < 0.001$), and is independent of sex ($F = 0.04$, $P > 0.05$; interaction term not significant, $F = 3.3$, $P > 0.05$). Rates of group 1 represent 60 ± 7% of the expected values (65 ± 8% for the 5 males and 58 ± 6% for the 13 females) and those of group 2 represent 44 ± 7% of expected (40 ± 4% for the 2 males and 46 ± 8% for the 4 females).

According to HEUSNER (1982), a scaling relationship of the form $a \, m^{-0.33}$, where *a* varies between species of different body mass, may be more appropriate for intraspecific comparisons of the mass-specific BMR. In each species, *a* can be determined by letting the scaling relationship pass through the averages of BMR and mass, and these can be obtained as the means of seasonal averages. Using this method, *a* is equal to 2.15 in the case of *N. humeralis* (Fig. 1). The effect of season on the scaled BMR remains highly significant ($F = 28.1$, $P < 0.001$), whereas the effect of sex ($F = 0.004$, $P > 0.05$) and the interaction term sex * season ($F = 3.0$, $P > 0.05$) are not significant. Bats of group 1 still have a significantly higher BMR than those of group 2 (114 ± 12% vs. 85 ± 14% of expected).

The oxygen consumption of adipose tissue is generally assumed to be lower than that of other tissues. Because the increased body mass of evening bats in group 2 is essentially due to fat accumulation, one may hypothesize that this is the cause of their reduced BMR. It is possible to test the most conservative (although biologically unrealistic) hypothesis, i.e. the one assuming that metabolism of adipose tissue is zero. According to this assumption, a scaling relationship of the form $b \, m^{-1}$ would be appropriate to describe the seasonal variation in BMR. The BMR of bats from group 2 would then fall on a line of equation 10.71 m^{-1}, which passes through the average BMR and mass of group 1 (Fig. 1). Even when so scaled, the BMR of bats from group 2 remains lower than the BMR of bats

from group 1 ($85 \pm 17\%$ vs. $100 \pm 13\%$; $F = 6.0$, $P < 0.05$), whereas the effect of sex ($F = 3.9$, $P > 0.05$) and the interaction term ($F = 1.4$, $P > 0.05$) are not significant. This shows that fat accumulation alone is unable to explain the reduction in the BMR of evening bats in group 2.
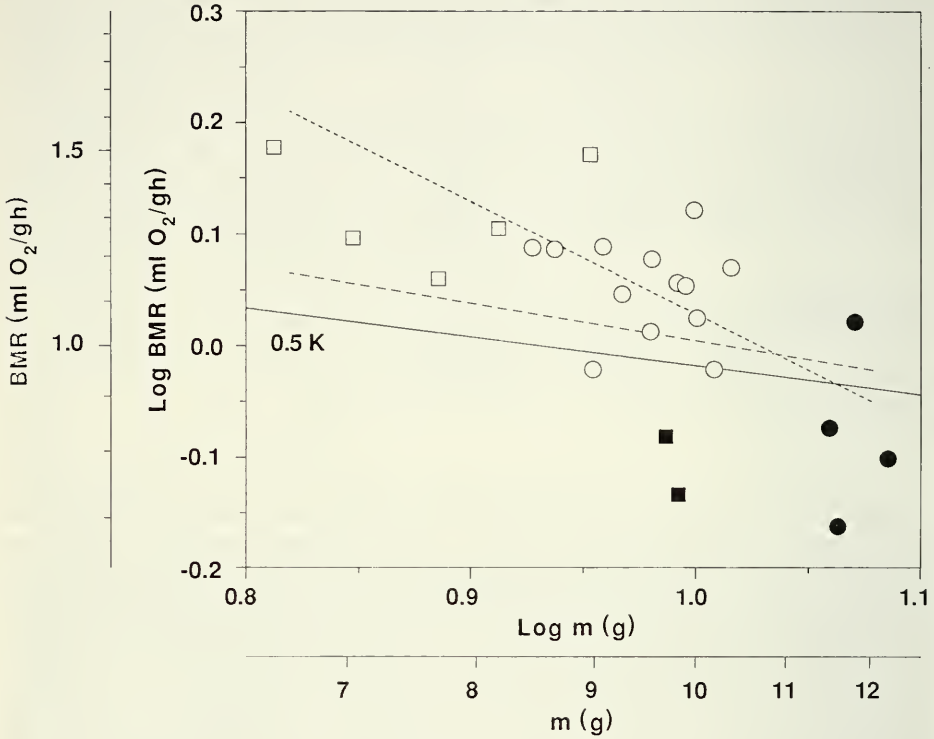

FIGURE 1.

Basal rate of metabolism (BMR) of *Nycticeius humeralis* as a function of body mass (*m*). Open symbols: group 1 (spring-summer). Closed symbols: group 2 (autumn-winter). Squares: males. Circles: females. 0.5 K: 50% of the Kleiber allometric relationship (3.42 $m^{-0.25}$). Dashed line: Heusner allometric relationship passing through the average BMR and body mass of groups 1 and 2 (2.15 $m^{-0.33}$). Dotted line: line of equation 10.71 m^{-1}, passing through the average BMR and mass of bats from group 1.

LASIURUS SEMINOLUS

As in *N. humeralis,* female *L. seminolus* were significantly heavier than males ($F = 16.3$, $P < 0.01$) (Table 1). Body mass in seminole bats also depended on season ($F = 5.6$, $P < 0.05$; interaction term sex * season not significant, $F = 3.4$, $P > 0.05$), but contrary to that of evening bats, it was slightly larger in group 1 than in group 2 (Table 1). The BMR ranged between 1.00 and 1.52 mlO_2/gh. Individuals of group 2 generally had
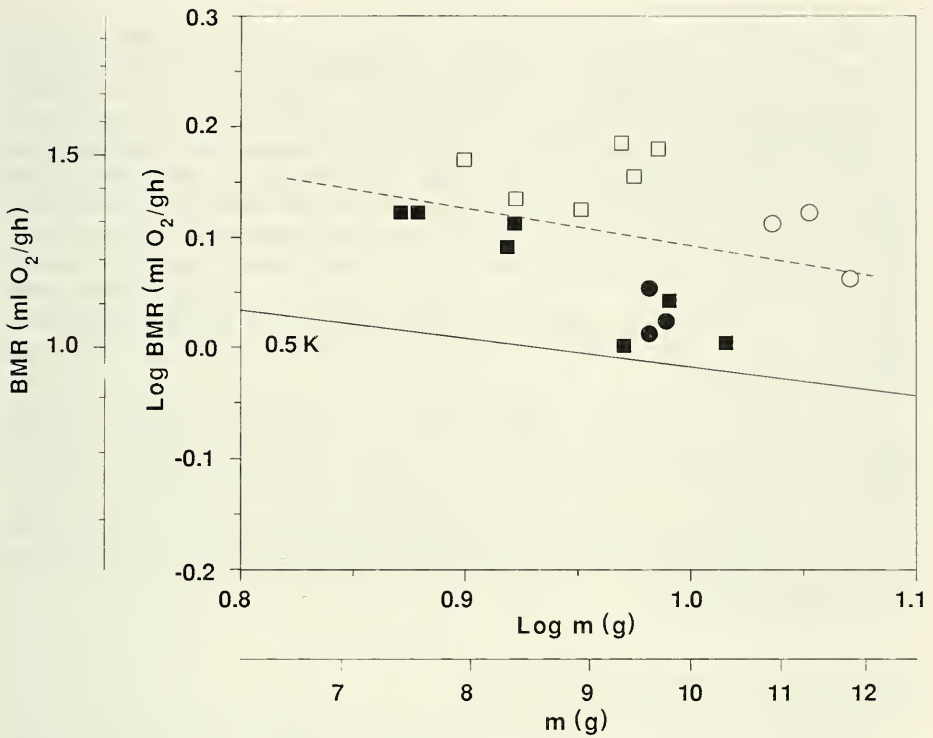
FIGURE 2.

Basal rate of metabolism (BMR) of *Lasiurus seminolus* as a function of body mass (*m*). Open symbols: group 1 (spring-autumn). Closed symbols: group 2 (winter). Squares: males. Circles: females. 0.5 K: 50% of the Kleiber equation (3.42 $m^{-0.25}$). Dashed line: Heusner allometric relationship passing through the average BMR and mass of groups 1 and 2 (2.65 $m^{-0.33}$).

lower rates than those of group 1 (Table 1 and Fig. 2), although their body mass was on average smaller. Furthermore, males tended to have slightly higher basal rates than females, and this may be explained by their smaller body mass. Again, the effect of body mass must be eliminated before differences due to season and sex can be tested.

If the measured basal rates are expressed as a percentage of the value expected from the KLEIBER relationship, BMR significantly depends on season ($F = 30.3$, $P < 0.001$), and is independent of sex ($F = 3.9$, $P > 0.05$; interaction term not significant, $F = 0.1$, $P > 0.05$). Rates of group 1 represent $71 \pm 5\%$ of the expected values ($73 \pm 5\%$ for the 6 males and $67 \pm 4\%$ for the 3 females) and those of group 2 represent $58 \pm 5\%$ of expected ($59 \pm 5\%$ for the 7 males and $55 \pm 3\%$ for the 3 females, Fig. 2). Furthermore, if using the HEUSNER scaling relationship (e.g. 2.65 $m^{-0.33}$ which passes through the general average of BMR and mass, Fig. 2), bats of group 1 still have a higher BMR than those of group 2 ($110 \pm 7\%$ vs. $89 \pm 7\%$) ($F = 35.1$, $P < 0.001$), whereas the effect of sex ($F = 2.7$, $P > 0.05$) as well as the interaction term ($F = 0.02$, $P > 0.05$) are not significant.

DISCUSSION

THE BMR OF NYCTICEIUS HUMERALIS AND LASIURUS SEMINOLUS

The evening bat *(N. humeralis)* and the seminole bat *(L. seminolus)* both have a depressed BMR: average basal rates between bats from groups 1 and 2 represent respectively 52% and 65% of the values expected from the KLEIBER relationship. These values agree with data available on other non-tropical insectivorous bats (LEITNER 1966, McNAB 1982, BOZINOVIC *et al.* 1985). The data presented in this paper also show a clear seasonal variation in the BMR of both species. This variation can be statistically demonstrated irrespective of the way used to account for variations in body mass within each species. The BMR of both species is indeed lower during the period where foraging activity is limited, i.e. during the autumn-winter period in *N. humeralis* and during the winter in *L. seminolus.*

In all analyses, sex had no significant effect on BMR, and a similar seasonal metabolic change was observed in both sexes. However, the number of individuals of each sex was relatively small and one cannot rule out a small sexual dimorphism in BMR. For example, in *L. seminolus,* a slight tendency for the males to have a higher BMR (independent of mass) than the females ($0.07 < P < 0.12$ depending on the allometric equation used) was observed. Furthermore, it should be stressed that females with an advanced pregnancy were excluded from the study and that only one lactating female (*L. seminolus,* with only one young) was measured.

SEASONAL VARIATIONS IN BMR IN MAMMALS

Any comparative study of the seasonal variations in BMR will be confronted with the difficulty of defining the "seasons". Depending on the habitat, seasonality may involve different parameters, such as temperature, rainfall and/or food availability. In addition, different species may adopt different strategies in response to the seasonal changes in their environment. For example, it is clear that changes in the level of foraging activity, which may be used as an indication of seasonal changes in food availability in temperate and sub-tropical bats, cannot be used as a general indicator of seasonality in mammals. In the following analysis, the variation in BMR between "winter" and "summer" is studied. As opposed to "summer", "winter" is considered as a period of the year of variable duration (usually some period within the months from October to April in the northern hemisphere) where ambient temperature is relatively low and food is usually less abundant. The choice of such a criterion of seasonality is obviously dictated in part by the availability of data, and particularly by the fact that all these data concern species inhabiting environments that exhibit a seasonality in temperature and, usually, food availability. According to this criterion, the groups 1 and 2 of the present study can be assigned to "summer" and "winter", respectively.

Various seasonal adjustments in the basal rate of metabolism have been described among mammals. However, as is the case for *N. humeralis,* such adjustments are often associated with simultaneous changes in body mass. Clearly, the observed variation in BMR may simply be the consequence of a change in body mass, or of a higher fat content rather than a metabolic adjustment *per se.*

Simultaneous changes in body mass have usually been accounted for by expressing BMR as a percentage of the value expected from the KLEIBER (1961) or BRODY (1945) scaling relationships. However, these equations are based on the comparison of species

averages, and may therefore not hold for intraspecific comparisons. Using 7 species of mammals, HEUSNER (1982) has shown that BMR scales to body mass in a different way within species than among species. Although HEUSNER's conclusions about the validity of the 0.75 exponent of the interspecific scaling relationship have been criticized with reason (FELDMAN & MCMAHON 1983), his results, together with the statistical analysis of FELDMAN & MCMAHON (1983), clearly suggest that an exponent of 0.67 (-0.33 for the mass-specific BMR) may indeed be more appropriate to describe intraspecific variations. However, the range of body mass within a species is usually narrow, so that the use of either of these scaling relationships to account for intraspecific mass differences leads to rather similar values.

The interpretation of seasonal variations in the BMR of different species showing simultaneous changes in body mass raises another problem. In some species the seasonal variations in body mass are mainly explained by changes in fat reserves, and in others not. Therefore, it seems doubtful that a single exponent could be used to describe the intraspecific scaling of BMR to body mass in all species. With this reservation in mind, one may at least obtain a tentative overview by comparing seasonal averages of the BMR once they are corrected for seasonal differences in body mass by expressing them as a percentage of the values expected from the HEUSNER scaling relationship. An index of seasonal variation in BMR may then be obtained as the difference between the average winter and summer percentages (Fig. 3). This index may slightly exaggerate BMR variations in species of which the seasonal changes in body mass are mainly explained by fat deposition. Mammals for which this index of seasonal variation can be calculated (Fig. 3) fall along a continuum ranging from species that have much lower rates in winter (negative index), to species that have higher rates in winter (positive index), and including species showing no seasonal variation in the BMR.

Comparative studies of the energetics of mammals have shown that the basal rate of metabolism is influenced by a number of factors and is particularily limited by high environmental temperatures, burrowing activity or low resource accessibility (MCNAB 1979a, 1987). In habitats characterized by high environmental temperatures and/or conditions that impede heat loss (e.g. still and moist air), a depressed BMR may clearly be an advantage because it increases heat tolerance and reduces the risk of overheating and/or water shortage (MCNAB 1966, 1979a, b, MACMILLEN & LEE 1970). Indeed, mammals inhabiting hot environments or closed burrows typically have low rates of metabolism, unless they are small (< 80 g). The pattern of seasonal variation in BMR observed among non-hibernating mammals living in warm habitats or in closed burrows (Fig. 3, open squares) is consistent with this interpretation. Among the 7 species for which an index of seasonality is available, six reduce their BMR in summer, when ambient temperature is highest. The exception is the desert fox *Vulpes macrotis* (GOLIGHTLY & OHMART 1983). Carnivores are certainly in a favourable position as desert dwellers, because of the high water content of their food (SCHMIDT-NIELSEN 1964). The desert fox shows that thermal factors may in some cases be outbalanced by other ecological factors (e.g. the maximization of reproductive effort; GOLIGHTLY & OHMART 1983).

A depressed BMR should also be selected in mammals feeding on food ressources that are either poorly accessible (either low availability or low digestibility) or undependable, because it decreases energy use and increases starving endurance. Species that respond to the winter food shortage by entering hibernation reduce their food intake to a minimum level, and should therefore select a low BMR to extend their starving endurance. Indeed, typical hibernators not only exhibit a rather low BMR, but also show a general tendency
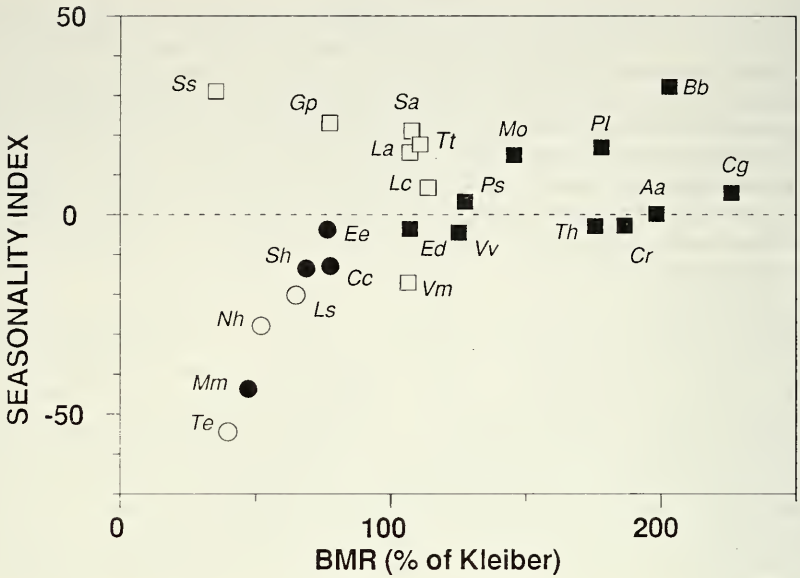
Index of seasonal variation in BMR of mammals (seasonality index = "winter" BMR-"summer" BMR; BMR of each species expressed as a percentage of the value expected from the Heusner relationship $a \, m^{-0.33}$ passing through the average BMR and mass of the species) as a function of the level of BMR (expressed as a percentage of the Kleiber scaling relationship). Dashed line: seasonality index = 0. Closed symbols: cold or temperate climates. Open symbols: warm climates. Squares: non-hibernating species. Circles: species entering hibernation or long term torpor. $Aa = Apodemus$ $agrarius$, $Bb = Blarina$ $brevicauda$, $Cc = Cricetus$ $cricetus$, $Cg = Clethrionomys$ $glareolus$, $Cr = Clethrionomys$ $rutilus$, $Ed = Erethizon$ $dorsatum$, $Ee = Erinaceus$ $europaeus$, $Gp = Geomys$ $pinetis$, $La = Lepus$ $alleni$, $Lc = Lepus$ $californicus$, $Ls = Lasiurus$ $seminolus$, $Mm = Marmotta$ $marmotta$, $Mo = Microtus$ $ochrogaster$, $Nh = Nycticeius$ $humeralis$, $Pl = Peromyscus$ $leucopus$, $Ps = Phodopus$ $sungorus$, $Sa = Sylvilagus$ $audubonii$, $Sh = Spermophilus$ $hudsonicus$, $Ss = Setifer$ $setosus$, $Te = Tenrec$ $ecaudatus$, $Th = Tamiasciurus$ $hudsonicus$, $Tt = Tayassu$ $tajacu$, $Vm = Vulpes$ $macrotis$, $Vv = Vulpes$ $vulpes$. (Data are from IRVING et al. 1955, KAYSER 1965, GORECKI 1966, 1969, HILDWEIN 1970, 1972, HILDWEIN & MALAN 1970, LYNCH 1973, HINDS 1973, 1977, ROSENMANN et al. 1975, ZERVANOS 1975, WUNDER et al. 1977, ROSS 1980, HELDMAIER & STEINLECHNER 1981, GOLIGHTLY & OHMART 1983, MERRITT, 1986).

to reduce it in winter (Fig. 3, open and closed circles), when food intake is lowest. One exception to this is the European hedgehog (*Erinaceus europaeus;* HILDWEIN & MALAN 1970).

The fact that *N. humeralis* and especially *L. seminolus* exhibit a seasonal variation in the BMR that is similar to that of hibernators should be stressed, because at least the second species certainly cannot be qualified as a hibernator in Florida. A number of other small mammals that are also subjected to seasonal fluctuations in their food resources and that also enter torpor (e.g. *Peromyscus leucopus*), do not exhibit a lower BMR in winter. One crucial difference appears to be the duration of the torpor bouts. Results of public shots, direct observations (CONSTANTINE 1958, JENNINGS 1958, BAIN & HUMPHREY 1986) and mist netting (personal observations) suggest that *L. seminolus* and *N. humeralis,* like

true hibernators, can spend extended periods in torpor (several days) and one may expect the selective force tending to reduce their rate of metabolism, and therefore to extend their starving endurance, to be directly related to the duration of their torpor bouts.

The seasonal variations in BMR that can be observed among non-hibernating mammals of cold and temperat regions appear less consistent (Fig. 3, closed squares). Several small species (e.g. *Peromyscus leucopus, Microtus ochrogaster, Blarina brevicauda*) increase their basal rate in winter, but in others (e.g. *Clethrionomys glareolus, C. rutilus, Apodemus agrarius, Phodopus sungorus*) no strong seasonal variation in BMR has been observed, as in the case for some larger arctic species (e.g. *Erethizon dorsatum, Vulpes vulpes, Tamiasciurus hudsonicus*). Clearly, many more data are needed to understand the pattern of seasonal variation in BMR observed in some small non-hibernating mammals of cold regions.

The influence of food habits and climate on the energetics of mammals has been demonstrated many times (reviews in McNab 1986, 1987). Recently, Elgar & Harvey (1986) have denied that food habits have a strong effect on BMR in mammals, arguing that the correlation between food habits and BMR could as well be described by taxonomic associations and that other factors associated with taxonomy may be more important. Intraspecific variations in BMR are free of these taxonomic complications. The basal rate of metabolism of many mammals does vary seasonally to a large extent, presumably permitting them to cope with the particular environmental conditions they meet in each season. Unfortunately, seasonal estimates of the BMR have at present been obtained only in a very small proportion of the mammalian species. However, consistent trends are already observed among species faced with extreme energetic conditions, e.g. those inhabiting hot environments or closed burrows, or hibernators. In these species, the observed pattern of variation can be consistently explained by the predominant influence of either thermal factors or resource accessibility. This suggests again that climate and food accessibility (among other factors) are important factors influencing the rate of energy expenditure in mammals.

Résumé

Les conditions climatiques et l'accessibilité de la nourriture figurent parmi les facteurs principaux qui influencent le métabolisme basal (BMR) des mammifères. Mais dans la plupart des habitats ces facteurs varient au cours de l'année. L'existence d'une variation saisonnière du BMR est examinée chez deux Chiroptères subtropicaux: *Nycticeius humeralis* et *Lasiurus seminolus*.

Les deux espèces ont un BMR bas (en moyenne 52% et 65% des valeurs prédites sur la base du poids corporel). Elles réduisent toutes deux leur BMR durant la période de

l'année où l'activité de fourragement est réduite (automne-hiver chez *N. humeralis* et hiver chez *L. seminolus*). Cette réduction peut être statistiquement démontrée quelle que soit la méthode utilisée pour éliminer l'influence du poids corporel. L'influence du sexe n'est au contraire pas significative.

Parmi les autres mammifères qui présentent une variation saisonnière du BMR, on peut distinguer: 1) les hibernants, chez lesquels le BMR varie de manière similaire aux deux espèces étudiées, 2) des mammifères d'habitats chauds, qui ont un BMR plus bas en été et 3) certains petits mammifères de régions froides ou tempérées, qui ont également un BMR plus bas en été. D'autres mammifères ne présentent pas de variation. L'influence des conditions climatiques et de l'accessibilité de la nourriture sur le BMR apparaît claire-ment chez les espèces de régions chaudes qui abaissent leur BMR lorsque la température est la plus élevée, ainsi que chez les hibernants, qui réduisent leur BMR lorsque l'apport de nourriture est réduit.

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